

ECOLOGY AND BEHAVIOUR OF ADULT BLACK FLIES (SIMULIIDAE): A REVIEW¹

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The assessment of simuliid abundance requires regular sampling of emerging, attacking and ovipositing adult flies throughout the season. An understanding of adult activities is needed to appreciate simuliid population dynamics, the impact of their biting on humans and animals, and their role as vectors of parasitic organisms. Some studies on simuliids are reviewed in relation to collection methods, mating, dispersal, orientation to hosts, oögenesis and need for a blood meal, and oviposition.

La mesure de l'abondance des simuliides demande un système dont on prend des échantillons réguliers de mouches adultes en état d'émergence et en train d'attaquer tantôt que de mouches oviposantes. Une connaissance des activités des adultes est impératif si on veut comprendre la dynamique des populations des simuliides, l'effet de leurs piqûres sur des humains et des animaux, et leur rôle comme porteurs de parasites. Ce que suit discute quelques études des méthodes de collection, comportement sexuel, dispersion, orientation vis à vis des hôtes, oögenèse et le requisite d'un repas de sang, et d'oviposition.

INTRODUCTION

Black flies, in addition to being notorious for their bloodsucking and consequent toxic effects, transmit protozoan and nematode parasites to domestic and wild birds as well as to mammals in North America and elsewhere (Fredeen 1977). Simuliids may even play some role as vectors of encephalitis viruses which they may propagate among birds and transmit to humans. In Wisconsin, black flies have been found to harbour Eastern Equine Encephalitis virus (Anderson *et al* 1961).

With these considerations and with the launching in 1974 of the 20-year WHO programme to combat River Blindness or Onchocerciasis in the Volta River watershed of West Africa, (UN Special Rep. 1973, p.v) research on the biology and control of black flies is expanding. An understanding of simuliid population dynamics and factors influencing simuliid distribution and activity, may assist in avoiding these pests and controlling them.

COLLECTING ADULT SIMULIIDS

Black flies breed in rivers and streams, the outlets of ponds and lakes being especially productive for filter-feeding larvae. There are many methods of sampling simuliid populations in order to assess their way of life and behaviour. The immature stages are sampled in a variety of ways (Wolfe and Peterson 1958; Wood and Davies 1966; Lewis and Bennett 1974), but this aspect falls outside the scope of this paper. For sampling emerging adults, Ide (1940) promoted cubic-yard mesh cages placed over the stream bottom. These allow continuous daily sampling throughout the season to assess changes in relative abundance of adults of different simuliid species with minimum disturbance to the habitat. Using this method in Ontario, Davies (1950) found that a square-yard of stream bottom at a lake outlet could produce between 60–100 thousand simuliid adults per year, mostly during late May and June. Another method for sampling emerging adults of both sexes, used successfully for *Simulium damnosum* and other species in Africa (Bellec 1974, 1976), consists of placing a square-meter aluminum

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sheet coated with sticky material, on the ground beside a stream, or suspending a sticky transparent square vertically above the stream at right angles to the stream flow (Bellec and Hebrard 1976). This method collects, in addition to emerging black flies, parous and gravid nulliparous females, and may prove successful with other simuliid species in North America.

Adult female simuliids are collected during their biting period in a number of ways: 1) using a cubic-screen cage attached, with the open end forward, on top of a vehicle which is driven along roads (Davies and Peterson 1956) at a determined speed and for a measured distance (Davies and Roberts 1973); 2) with an insect net swept around humans or ruminants in a prescribed manner (Davies 1952; Golini *et al* 1976); 3) exposing a bird or mammal for a certain time, then covering it periodically with a fine-mesh cage from which flies are aspirated (Mondchadskij and Radzivilovskaya 1948; Bennett 1960; Anderson and DeFoliart 1961; Herman and Bennett 1976), or exposing animal product such as ground beef and tallow (Davis and James 1957); 4) placing a steer in a screened box-trap with open louvres (Roberts 1965); 5) using sticky models of mammals (Fredeen 1961) and birds, activated from a distance by strings (Wenk 1962; Wenk and Schlörer 1963) or baited with CO₂ (Fallis *et al* 1967; Golini 1970, 1975b; Fallis and Raybould 1975); 6) with suction fan-traps, baited with CO₂ (Fallis and Smith 1964; Smith 1966; Fallis *et al* 1967; Golini 1970); and 7) with a light trap at night. Some simuliids may be collected at night with an incandescent light trap (Williams 1964; 1965), but the catch is usually much larger with a UV or "black" light trap (Williams and Davies, 1957; Grebelskij *et al* 1963; Davies 1975).

MATING

After adult simuliids emerge, they rest near the stream before dispersing away from their breeding site, the distance of dispersal depending on the species, the density and height of ground cover, and weather conditions. They may feed first on nectar of flowers (Hocking 1953, Davies and Peterson 1956) and then mate. Nearly all females examined after capture from live animals or CO₂-baited traps are found to be inseminated (Lewis 1957; Wenk 1965; Arkhipova 1966; Rühm 1970; Pascuzzo 1976), indicating that mating may be a releasing stimulus to host seeking.

Before mating, males usually form swarms over some conspicuous marker: the top of a tree or stump, the corner of a building, a dam or base of a waterfall, an open patch of ground, or roadway (Davies *et al* 1962, p. 76; Downes 1969). However, males of some species swarm below a marker (Wenk 1965). Males of most species have eyes with larger dorsal facets which may be adapted for detecting small objects moving above them (Davies and Peterson 1956, Kirschfield and Wenk 1976). Females flying above such male swarms are chased and mated with; many coupled pairs fall to the ground (Hocking and Pickering 1954; Peterson 1962). I have flicked minute pebbles into a small swarm from below and elicited a chase reaction only when the pebble arced above the male swarm. Males of a few species, e.g. *Cnephia dactoneis* Dyar and Shannon, possess eyes with reduced dorsal facets and mate mainly while crawling on the ground near the stream without a flying swarm (Twinn 1936; Nicholson 1945; Davies and Peterson 1956).

DISPERSAL

To estimate time and place of simuliid attacks, it is necessary to know the distance black flies will disperse from their breeding sites and how meteorological factors influence their dispersal. Various dispersal distances have been reported in Canada: 95–160 km in the prairies (Rempel and Arnason 1947), shorter distances in boreal forest, ranging from 3–8 km (Bennett

1963, Bennett and Fallis 1971) and 8.5–35 km (Baldwin *et al* 1975). Warm moist air currents will undoubtedly enhance dispersal of simuliids, especially in open and unprotected areas; and black flies have been captured at a height of 1500 m from an aircraft over Mississippi (Glick 1939). Weather conditions that maximize and minimize flight dispersal should be understood. Maximum flight activity of female *Simulium venustum* Say¹ occurs in light winds with low atmospheric saturation deficiency (=high relative humidity), air temperatures between 15–25 C and rapidly changing, especially falling, atmospheric pressure (Davies 1952). Such was found in other species (Underhill 1940), and simuliid females are influenced as well by incident light intensity (Wolfe and Peterson 1960).

HOST ORIENTATION

Black flies appear to find a vertebrate host and complete their blood meal through a series of behavioural steps which may include the following (Smith 1966, Golini 1970).

- a. Activation Flight through intrinsic factors (e.g. hunger) or extrinsic factors (e.g. changes in wind speed, atmospheric pressure or light).
- b. Random flying.
- c. Far-distance orientation (by olfaction).
- d. Middle-distance orientation (olfaction plus vision); bright colours contrasting with background; moving objects.
- e. Near orientation (mainly vision – dark colours).
- f. Landing (mainly vision as in “e”).
- g. Crawling and probing (olfaction and gustation).
- h. Piercing and feeding (gustation).
- i. Withdrawl and leaving the host.
- j. Resting and digesting the blood meal.

In addition, females of some simuliid species have a specific habitat preference which is usually associated with a specific host on which they feed. Certain species (e.g. *Simulium anatinum* (Wood), *S. euryadminiculum* Davies, *S. rugglesi* Nicholson & Mickel) remain close to bodies of water, seldom flying higher than 2 m, and feed mainly on ducks and loons (Davies and Peterson 1957; Bennett 1960; Anderson and DeFoliart 1961; Golini 1970, 1975b). Other species disperse farther from the water and may show preferences for open or wooded areas, and for certain heights above ground, depending on the type of vegetational cover, the time of day and weather conditions, especially wind and incident light (Bennett 1960; Wolfe and Peterson 1960; Smith 1966; Golini 1970; Patrusheva 1972; Pascuzzo 1976).

Both olfaction and vision are important in host finding. Odour can increase frequency of spontaneous flying in female mosquitoes (Daykin *et al* 1965). It has been postulated that female mosquitoes fly randomly, drifting downwind until stimulated by an olfactory cue from a host. Then they fly more actively upwind as long as their upwind flight is reinforced by scent (Wright 1958) and they must orient to a ground pattern (Kennedy 1939). A similar host-finding mechanism has been proposed for simuliids (Smith 1966). *S. venustum* females are known to fly upwind toward a source of CO₂; although CO₂ appears to activate flies only over a short distance, not farther than 5 m when the gas is released at 300 cc/min (Golini and Davies 1971). This response to CO₂ has been observed in other simuliid species (Bennett *et al* 1972). Females of *S. euryadminiculum* are highly host specific, being attracted exclusively to the uropygial oil of loons (Lowther and Wood 1964). Other species are attracted to duck oil in combination with CO₂, or to CO₂ alone (Fallis and Smith 1964, Golini 1975b). In addition, Brown (1966) found that certain amino acids (lysine and alanine), when warmed to 37 C and

¹Known now to be a species complex (K.H. Rothfels *pers comm*).

combined with CO₂, increased attraction of simuliids more than CO₂ alone, as has been found also for mosquitoes (Brown and Carmichael 1961).

Golini (1970) and others have found that certain simuliid species are more attracted to large silhouettes, hence these species attack more often large mammals (Golini *et al* 1976); while other species which are attracted to small silhouettes are presumed to attack small birds or mammals (Anderson and DeFoliart 1961; Wenk and Schlörner 1963; Golini 1970; Fredeen 1961). Wenk and Schlörner (1963) found also that moving models were more attractive to host-seeking simuliids. Similarly, bright colours, sharply contrasting with the background, also may attract black flies from a distance (Fallis and Smith 1964; Fallis *et al* 1967; Bradbury and Bennett 1974). At short visual range host-seeking females of *S. venustum* are attracted to, and land on, dark grey in preference to black, light grey or white, and on colours such as dark maroon and purple, while they are repelled by green, yellow and orange especially in lighter tones (Davies 1972). It is also known that twice as many females of *S. venustum* land on the shaded darker side of a human host than on the lighter sunny side, and of those that land, twice as many bite on the shaded side (Davies 1952; Anderson and DeFoliart 1961). Biting of those that land increases significantly during periods of rapidly changing, especially falling, atmospheric pressure (Davies 1952). The maximum attack of *S. venustum*, found in one study in Algonquin Park, Ontario, occurred in mid June 1947 when the landing rate on a human reached 78 flies/6.5 cm²/min and the biting rate 17 flies/6.5 cm²/min (Davies, D.M. unpubl. notes).

AUTOGENY AND ANAUTOGENY

Simuliid species are grouped into three physiological types based on nutritional requirements of females for egg development (Davies, Györkös and Raastad 1977).

I. Species whose females have reduced mouthparts and are unable to feed on blood. They use nutrients carried over from larvae for their single gonotrophic cycle; these are autogenous species (e.g., *Gymnopais* spp., *Prosimulium gibsoni* (Twinn), *Twinnia tibblesi* Stone & Jamnback, *Cnephia dacotensis*).

Autogenous females with reduced mouthparts often emerge with eggs mature, or nearly so. Such females mate close to the stream, often while crawling, and oviposit shortly thereafter (Davies and Peterson 1956; Davies *et al* 1962). This short adult life seems to be an adaptation of some subarctic species faced with harsh terrestrial weather conditions (Downes 1965). Adaptation has evolved further to parthenogenetic species with eggs sometimes hatching from disintegrating parhate females, their development halted within the pupal skin by termination of the short warm season (Carlsson 1962).

II. Species whose females have biting mouthparts but usually produce the first batch of eggs without a blood meal; such females are autogenous for their first gonotrophic cycle (e.g., *P. fuscum* Syme & Davies, *C. mutata* (Malloch), *S. decorum* Walker, *S. vittatum* Zetterstedt). However, these females require a blood meal for subsequent gonotrophic cycles (Davies 1961; Pascuzzo 1976; Davies D.M., unpubl. notes). Sometimes autogeny may not be attained during the first cycle, especially in small females, if during larval life food was scarce and temperature high (Rubtsov 1956; Chutter 1970; Pascuzzo 1976).

Females of species autogenous for the first cycle, after mating, rest in vegetation usually near the stream for 3–4 days until eggs mature, and after successful oviposition may fly off in search of a blood meal (Davies 1961).

III. Species, whose females require a blood meal to produce any eggs, are known as anautogenous (e.g., *P. mixtum* Syme & Davies, *S. venustum*).

In fully anautogenous species, newly emerged females may spend 1–2 days mating and

feeding on nectar before seeking a host (Davies and Peterson 1956). After a blood meal, digestion and oögenesis takes 3–8 days depending on the temperature. Saliva, midgut digestive enzymes, the peritrophic membrane, and digestion of blood and sugars in simuliids have been studied (Yang and Davies 1968a, b; 1974; 1977), and also studies have been made on ovarian development (Madahar 1967; Chen 1969; Liu *et al* 1975; Pascuzzo 1976).

Certain reproductive functions have been shown to be enhanced in larger females (Pascuzzo 1976), as follows:

1. Potential Fecundity - number of ovarioles at eclosion
2. Actual Fecundity - number of eggs matured
3. Potential Fecundity Realized - percentage of ovarioles producing mature oöcytes
4. Stage of Ovarian Development at Adult Eclosion
5. Size of Mature Eggs

OVIPOSITION

Eggs are usually deposited near sunset, but oviposition may occur at other times of the day when there are heavy clouds, warm moist air, light wind and rapidly changing air pressure (Davies 1952). Females of some species oviposit while in flight by tapping the water surface and releasing one or more eggs. Females of other species lay eggs in midstream and still others in shallow microbays. In certain species, if it is too windy, females will seek refuge in a crevice at the water's edge and lay eggs in loose strings into the water. Others normally lay eggs on floating green or yellow vegetation or on solid substrates lapped by or under water (Davies and Peterson 1956; Wolfe and Peterson 1959; Golini and Davies 1975a, b; Golini 1975a). Females of some species lay more eggs on substrates of certain colours, i.e., white, yellow, and light green (Peschken and Thorsteinson 1965; Golini and Davies 1975a, b; Golini 1975a); these are the colours least attractive to certain species when seeking blood (see above).

NUMBER OF GENERATIONS

The number of generations per year depends on the species. Fully autogenous species are usually univoltine and this is true for certain species that are autogenous for only the first ovarian cycle or anautogenous. Other species which may breed continually in subtropical and tropical climates, have four or more generations per year, whereas for the same species in temperate and subarctic climates the number of generations may be reduced to one or two. However, it may be difficult to determine the number of generations when females of some species have more than one ovarian cycle, up to five according to Shipitsina (1962) and Lebed (1959).

It is hoped that this brief review, incorporating some new observations and hypothesis, will stimulate further research into simuliid behaviour and ecological relationships.

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